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Name Changes in the "Acmaeidae"

by

DAVID R. LINDBERG

Museum of Paleontology, University of California, Berkeley, California 94720, U.S.A.

Abstract. Major changes at the familial and generic level in the "Acmaeidae" are introduced here. These changes are necessary because morphological convergence in limpet taxa has been greatly underestimated, and the previous classifications have failed to recognize many of the distinct lineages in the taxon. Three new taxonomic changes are presented and discussed: (1) The division of the family Acmaeidae into two families, the Acmaeidae, which contains the genera *Acmaea* and *Pectinodonta,* and the Lottiidae, which includes the remaining genera previously assigned to the family Acmaeidae. (2) The synonymization of the genus *Collisella* with the senior synonym *Lottia.* (3) The restriction of the genus *Notoacmea* to Australian and New Zealand species and the referral of the remaining species to the genus *Tectura.*

INTRODUCTION

NAME CHANGES of well-known or well-studied taxa always generate skepticism, resentment, and frustration in the biological community. Moreover, they add another entry for bibliographic searches and create longer, more elaborate synonymies. However, as the understanding of phylogenies increases, the necessary name changes must be made. And because the valid name is determined by rules of nomenclature, the correct name may not be our "favorite."

Detailed studies of members of the family Acmaeidae Forbes, 1850, show that phylogenetic relationships are poorly reflected in the current classification and that a thorough revision of the group is needed. Three contributions toward that revision have appeared (LINDBERG, 1981a, 1983; LINDBERG & MCLEAN, 1981). Much of this work is synthesized and incorporated in the forthcoming *The Archaeogastropoda of the Northeastern Pacific* (J. H. McLean & D. R. Lindberg). Also appearing in that volume are radical changes in patellacean taxonomy at the generic and familial levels. Because of the constraints of the systematic format in that work, it was not possible to discuss in detail all the factors involved in many of these changes. Therefore, I present here discussion of three of the more disconcerting changes: (1) the division of the family Acmaeidae into two families, the Acmaeidae Forbes, 1850, and the Lottiidae Gray, 1840; (2) the synonymization of the genus *Collisella* Dall, 1871, with the senior synonym *Lottia* Sowerby, 1834; and (3) the transfer of eastern Pacific limpets from the genus *Notoacmea* Iredale, 1915, to the genus *Tectura* Gray, 1847. Reasons for the chronic taxonomic confusion in these limpets are also discussed. It is hoped that these explanations will ease the tension during the transition. A summary of name changes proposed here for the northwest Pacific "Acmaeidae" is presented in Table 1.

LOTTIIDAE GRAY, 1840, AND ACMAEIDAE FORBES, 1850

There always has been something enigmatic about *Acmaea mitra* Rathke, 1833, the type species of the genus *Acmaea* Eschscholtz. IREDALE (1915) proposed four genera for the New Zealand acmaeid fauna because he could not find any similarities between the New Zealand species and the northeastern Pacific type species. Had Iredale compared any of the New Zealand species to any other northeastern Pacific species, he would have found at least two apomorphic characters in either shell morphology, shell structure, radula configuration, or radular basal plate morphology shared between the species in hand. In 1950 J. A. Shotwell found that *A. mitra* was an exception to a general trend in shell morphology relative to height in the intertidal zone in northeastern Pacific "*Acmaea*" (SHOTWELL, 1950). More recently, MARGOLIN (1964) has pointed out that, unlike other low intertidal "acmaeids," *A. mitra* does not have an escape response from the predatory starfish *Pisaster ochraceus* (Brandt, 1835).

Although there has been little general agreement among patellacean systematists, almost all workers have restricted the usage of the genus *Acmaea. Acmaea* was one of four names intended to include all patellaceans with a single

Table 1

Summary of name changes for the northwest Pacific "Acmaeidae."

Old classification (LINDBERG, 1981b)	New classification
Family Acmaeidae Forbes, 1850	Family Acmaeidae Forbes, 1850
Acmaea mitra Rathke, 1833	*Acmaea mitra* Rathke, 1833
	Family Lottiidae Gray, 1840
Acmaea funiculata (Carpenter, 1864)	*Niveotectura funiculata* (Carpenter, 1864)[1]
Acmaea apicina Dall, 1879	*Erginus apicina* (Dall, 1879)[1]
Problacmaea moskalevi Golikov & Kussakin, 1972	*Erginus moskalevi* (Golikov & Kussakin, 1972)[1]
Problacmaea sybaritica (Dall, 1871)	*Erginus sybaritica* (Dall, 1871)[1]
Lottia gigantea Sowerby, 1834	*Lottia gigantea* Sowerby, 1834
Collisella pelta (Rathke, 1833)	*Lottia pelta* (Rathke, 1833)
Collisella digitalis (Rathke, 1833)	*Lottia digitalis* (Rathke, 1833)
Collisella paradigitalis (Fritchman, 1960)	*Lottia strigatella* (Carpenter, 1864)
Collisella conus (Test, 1945)	*Lottia conus* (Test, 1945)
Collisella limatula (Carpenter, 1864)	*Lottia limatula* (Carpenter, 1864)
Collisella ochracea (Dall, 1871)	*Lottia ochracea* (Dall, 1871)
Collisella triangularis (Carpenter, 1864)	*Lottia triangularis* (Carpenter, 1864)
Collisella instabilis (Gould, 1846)	*Lottia instabilis* (Gould, 1846)
Collisella alveus (Conrad, 1831)	*Lottia alveus* (Conrad, 1831)
Collisella asmi (Middendorff, 1847)	*Lottia asmi* (Middendorff, 1847)
Collisella borealis Lindberg, 1982	*Lottia borealis* (Lindberg, 1982)
Tectura rosacea (Carpenter, 1864)	*Tectura rosacea* (Carpenter, 1864)
Notoacmea testudinalis (Müller, 1776)	*Tectura testudinalis* (Müller, 1776)
Notoacmea scutum (Rathke, 1833)	*Tectura scutum* (Rathke, 1833)
Notoacmea persona (Rathke, 1833)	*Tectura persona* (Rathke, 1833)
Notoacmea fenestrata (Reeve, 1855)	*Tectura fenestrata* (Reeve, 1855)
Notoacmea paleacea (Gould, 1853)	*Tectura paleacea* (Gould, 1853)
Notoacmea depicta (Hinds, 1842)	*Tectura depicta* (Hinds, 1842)
"*Notoacmea*" *insessa* (Hinds, 1842)[2]	
"*Collisella*" *scabra* (Gould, 1846)[2]	

[1] See LINDBERG, 1983.

[2] Generic classification will be discussed elsewhere; "*N.*" *insessa* is a member of the family Lottiidae, "*C.*" *scabra* is not.

gill in the nuchal cavity. After 40 years of indiscriminate use of *Acmaea* and the other three names (*Lottia*; *Patelloida* Quoy & Gaimard, 1834; and *Tectura* Gray, 1847), DALL (1871) first revised the Acmaeidae, based on shells, radulae, and external anatomy of 32 species. He was the first to define subgenera, based primarily on radular characters. After this initial splitting, generic and subgeneric names proliferated in the family. The increasingly restricted use of the name *Acmaea* s.s. results in a current definition that usually includes fewer than five species. However, as discussed below, *Acmaea* is monotypic. And not only is *A. mitra* the only species, it is also distinct at the familial level from all other putative intertidal acmaeids; the relatives of *A. mitra* are in the subtidal, not the intertidal.

MACCLINTOCK (1967:75) was the first to point out that *Acmaea mitra* and members of the predominately subtidal family Lepetidae Gray, 1857, belong to the same shell-structure group (his group 15): "no other patelloid currently classed in the family Acmaeidae is known to have a shell structure similar to that of *A. mitra*." But how could *A. mitra* be related to blind, gill-less, subtidal limpets with bizarre radulae? An important pattern was recognized when members of the patellacean genus *Pectinodonta* Dall, 1882, were found to also be members of shell structure gorup 15 (LINDBERG, 1981a). Members of the genus *Pectinodonta* are blind, gill-bearing, subtidal limpets with bizarre radulae. However, there are important plesiomorphic characters shared by *A. mitra* and species of *Pectinodonta*. Besides shell structure, both share three pairs of lateral teeth arranged in a posteriorly diverging ∧-shape, identical ventral plate morphology, a lack of marginal teeth, and similar gross anatomy and shell morphology. The major differences between the two taxa are the lack of eyes and the multicuspid third lateral teeth of *Pectinodonta*. The lack of eyes in abyssal species is common in marine mollusks and other invertebrates, and a similar multicuspidate modification of the third lateral teeth for feeding on wood is also known in *Potamacmaea* (PEILE, 1922) from southwest Asia, a member of the subfamily Patelloidinae (OLIVER, 1926) (Lindberg, unpublished observation). Thus, the differences between *Acmaea* and *Pectinodonta* are minor compared to the differences between these two taxa and the other members of the family "Ac-

maeidae." Moreover, the similarities between these two white-shelled genera and the white-shelled Lepetidae are becoming apparent as the progenetic nature of the Lepetidae is recognized (McLean & Lindberg, in preparation).

Restriction of the genus *Acmaea* to a single species and the newly recognized phylogenetic relationship between *Acmaea, Pectinodonta,* and the Lepetidae, which constitute distinct taxa of the familial category (*i.e.*, Lepetidae and Pectinodontinae Pilsbry, 1891), necessitate a reconsideration of the family Acmaeidae and its place in classification. The family Acmaeidae must be redefined to reflect more accurately the phylogeny of its clade. The family is, therefore, redefined to include two subfamilies, the Acmaeinae and the Pectinodontinae. The type genera are the only genera referred to these subfamilies. The Lepetidae are maintained as previously defined by McLean (1966) and Moskalev (1977). Those taxa previously assigned to the family Acmaeidae that are not members of shell-structure group 15 are referred to the family Lottiidae Gray, 1840 (type genus *Lottia* Sowerby, 1834), the oldest available name for this clade. The shells of members of the families Lottiidae, Lepetidae, and Acmaeidae always have radial and concentric crossed-lamellar layers in juxtaposition. In the families Lepetidae and Acmaeidae, a foliated layer is always present dorsal of the concentric crossed-lamellar layer; the Lottiidae lack a foliated layer.

Lottia Sowerby, 1834, *vs. Collisella* Dall, 1871

In 1833 J. E. Gray proposed the genus *Lottia,* diagnosing it as follows: "[*Lottia*] must be extremely perplexing to those systematists who attend only to the form of the shells without paying any regard to its animal inhabitant. The shells of *Patella* and *Lottia* do not in the least differ in external form, and yet their animals belong to very different orders, the one having the branchiae placed around the foot as in chitons, and the other having them placed on the side of the neck, like the Fissurellae, from which indeed it chiefly differs in having only one branchia" (Gray, 1833:800). From this description it is clear that Gray recognized the distinctness of the clade that has been subsequently known as the Acmaeidae. In a 4-yr period (1830 to 1834) other names in this group were introduced: Tecture by Audouin & Milne-Edwards (1830), *Acmaea* by Eschscholtz (1833), *Lottia* by Gray (1833), and *Patelloida* by Quoy & Gaimard (1834). Although the respective type species differed in radular characters, distinctions were not made at the time. It remained for Dall (1871) to recognize their differences.

In 1871 W. H. Dall proposed the subgenus *Collisella* (type species *Acmaea pelta* Rathke, 1833) for those acmaeid limpets with a single pair of reduced marginal teeth (uncini) and a ctenidium (Dall, 1871). In the late 1940's Japanese workers had begun to use *Collisella* as a full genus based on radular and shell characters. McLean (1966) followed this trend, recognizing *Collisella* at the generic level based on radular, shell, and ecological criteria. Many subsequent workers followed this usage, and with the publication of *Light's Manual* (Smith & Carlton, 1975), the use of *Collisella* became well-established in literature on northeastern Pacific intertidal species.

Although Gray originally diagnosed the genus *Lottia* by the single gill in the nuchal cavity, this distinction was lost because he failed to provide an indication of the taxon (Article 16; ICZN, 1964). Sowerby (1834) validated *Lottia* when he published a description of the genus and illustrations of four species, *L. gigantia, L. antillarum, L. testudinaria,* and *L. radians.* When Sowerby illustrated *L. gigantea* he had no idea that the animal that inhabited the shell also had a secondary gill. He used the genus *Lottia* in Gray's original sense, for those limpets with a nuchal cavity gill rather than a secondary gill. It was J. G. Cooper who in 1860 first brought to P. P. Carpenter's attention the presence of both a nuchal cavity gill and a secondary gill in this enigmatic species. Carpenter (1860) proposed the genus *Tecturella* for this species with both "acmaeid" and patellid gill characters. However, *Tecturella* was a homonym of *Tecturella* Stimpson, 1853, a genus of polychaete worms. In 1861 Carpenter proposed *Tecturina,* possibly as a replacement name for *Tecturella* (Carpenter, 1861), but failed to diagnose the genus and thus *Tecturina* must be regarded as a *nomen nudum.* Carpenter had one more go at it in 1866 when he proposed the genus *Lecania*; however, he had realized by 1864 (Carpenter, 1864:650) that the genus *Lottia* was available for this species because of Sowerby's (1834) illustration of *L. gigantea,* and thus he published *Lecania* in synonymy with *Lottia.* Therefore, *Lecania* is Carpenter's second *nomen nudum* for the taxon. It is also a homonym for *Lecania* Macquart, 1839, a genus of Diptera. Carpenter (1866:344) did, however, establish *L. gigantea* as the type species of *Lottia* by subsequent monotypy. Gray's (1847) designation of *Acmaea scutum* Rathke, 1833, as the type species of *Lottia* was not valid because *A. scutum* was not a species assigned by Sowerby to *Lottia* in his validation of Gray's name. Thus, the genus *Lottia* became restricted from Gray's original usage for limpets with a nuchal cavity gill to those with both a nuchal cavity gill and a secondary gill.

With the restriction of the genus *Acmaea* to limpets with conical, white shells and three pairs of radular teeth, the genus *Collisella* became the genus of choice for those limpets with a radular morphology identical to that of *Lottia,* but which lack secondary gills. Because gill morphology was considered to be the most conservative character in patellacean systematics, the obvious similarity between members of the genus *Collisella* and *L. gigantea* was never addressed.

Lindberg & McLean (1981) described four new species of *Lottia* from the Galápagos Islands. Although there was little similarity between these species and the large Californian *L. gigantea,* they pointed out that all five species shared a common shell structure, radula configu-

ration, and secondary gill morphology. Moreover, they pointed out that secondary gill morphology was not as conservative as once thought, and that shell structure was a much more reliable character. "Acmaeid" limpets with secondary gills have subsequently been found in the boreal, Panamic, and Caribbean regions (LINDBERG, 1983; personal observation). Moreover, these species belong to different shell-structure and radular groups, which strongly suggests that secondary gills have evolved in many different lineages and are, therefore, convergent characters. The obvious questions are: from what lineage did *L. gigantea* evolve, and is presence of a secondary gill a character of generic importance in this clade?

The answer to the first part of the question was furnished by comparing the anatomy and allozymes of *Lottia gigantea* to other California *Collisella* species. The results show that *L. gigantea* is very closely related to *Collisella limatula* (Carpenter, 1864) (SLY, 1984; Lindberg & Sly, in preparation). Moreover, *L. gigantea, C. limatula,* and *Collisella strigatella* (Carpenter, 1864) are more closely related to one another than they are to *Collisella pelta,* the type species of the genus *Collisella.* There is little doubt that *L. gigantea* is derived from *C. limatula* or from a common ancestor. Based on the fossil record of southern California and northern Baja California this speciation event occurred within the last 250,000 yr (Lindberg, unpublished data).

Thus, *Lottia gigantea* is the product of a recent speciation event within the *Collisella* group and is more closely related to some *Collisella* species then some *Collisella* species are to each other. The unique characters of *L. gigantea* all appear to be associated with the evolution of its territorial behavior (see STIMPSON, 1970, and WRIGHT, 1982, for a description of territorial behavior). The low profile shell with its strongly anterior apex forms a plowlike anterior slope that the limpet uses to push intruders out of its territory. The large size of this species, a common feature of territorial species (GHISELIN, 1974:142), undoubtedly presented problems of respiratory surface area to body volume, and the secondary gill was the evolutionary solution. These few autapomorphic characters are far outweighed by the symplesiomorphies in radular morphology, internal anatomy, shell structure, and external pigmentation.

The synonymizing of *Lottia* with *Collisella* has larger ramifications because *Lottia* is the senior synonym and all the species presently assigned to the genus *Collisella* should be assigned to *Lottia.* In many ways it is appropriate for *Lottia* to become the correct name for this diverse clade of limpets. After all, this usage exactly expresses the original intentions of J. E. Gray, who first recognized the group.

Tectura Gray, 1847, or *Notoacmea* Iredale, 1915

Notoacmea (type species, by original designation, *Patelloida pileopsis* Quoy & Gaimard, 1834) was proposed by IREDALE (1915) for several Australian species that were not referable to genera that he had earlier described. Although the criteria for the establishment of this genus were poorly defined, the name was adopted by Australian, New Zealand, and Japanese workers for fine-ribbed, thin-shelled species that lacked radular marginal teeth.

GRANT (1937:15) was the first worker to assign some of the northeastern Pacific "acmaeids" to *Notoacmea,* which she considered as a subgenus of *Acmaea.* FRITCHMAN (1961) adopted Grant's classification and published subgeneric assignments for many of the northeastern Pacific species. MCLEAN (1966) also used *Notoacmea* as a subgenus and then later (MCLEAN, 1969) considered *Notoacmea* as a full genus. However, there are problems with the use of *Notoacmea* for species outside the austral region. All new world "*Notoacmea*" have MACCLINTOCK's (1967) shell-structure group 1, whereas most of the *Notoacmea* of Australia and New Zealand have group 4.

In his study of the shell structure of the patellaceans, MACCLINTOCK (1967) found that shell-structure group 4 (includes group 5 also) were restricted to Australia and New Zealand. Those species with this unique shell structure include the type species of *Notoacmea* as well as the nominal genera *Atalacmea* Iredale, 1915, and *Conacmea* Oliver, 1926. Nowhere else in the world has this shell-structure type been found in either fossil or Recent species. Although it is apparently derived from shell-structure group 1 by a simple transposing of the radial crossed-lamellar layer to either side of the myostracum, it has a very limited biogeographical distribution.

I have earlier pointed out the problems with the use of *Notoacmea* for eastern Pacific species (LINDBERG, 1976, 1981b). However, a solution to this problem was not forthcoming because of the confusing character states found in several different groups of patellaceans for which the radula lacked marginal teeth. LINDBERG & MCLEAN (1981) established that it was possible to distinguish some of the groups by examining the complexity of the radular basal plates in different shell-structure groups (see also GRANT, 1937:14). They also pointed out that some eastern Pacific "*Notoacmea*" had thicker, more prominently ribbed shells than the typical *Notoacmea* of the austral region. As shell structure and radula configuration became known for additional eastern Pacific species, it was readily apparent that a clade of "acmaeids," convergent in radular morphology with *Notoacmea* in the austral region, was extant in the North Pacific, North Atlantic, and Caribbean regions. The determination of the correct name for this clade concerns us here.

Several type species are members of this clade, including *Notoacmea scopulina* Oliver, 1926 (*Subacmea* Oliver, 1926), *Patella testudinalis* Müller, 1776 (*Testudinalia* Moskalev, 1966), and *Patella virginea* Müller, 1776 (*Tectura* Gray, 1847). Although *Tectura* is the senior synonym for this clade, it was also the most unlikely genus given its current usage.

The concept of *Tectura* has most recently been restricted to small subtidal limpets with light-colored shells marked

with red or pink rays and with faint radial ribbing. The radular teeth of these species are approximately equal in size and shape; marginal teeth are lacking. There is a single gill in the nuchal cavity and members of this genus belong to shell-structure group 1. Previously, there have been only two species that were unquestionably members of this group, *T. virginea* and *T. rosacea* (Carpenter, 1864). Both are subtidal species and are associated with coralline algae. It is now recognized that equal development of the lateral teeth is a common adaptation of subtidal coralline-feeding species and that species with this radular type occur in almost every shell-structure group in the family Lottiidae (McLean, 1966; Lindberg, 1981b, 1983; Lindberg & McLean, 1981). It is, therefore, regarded as a convergent character in the family and of little use in systematics. This is also true of shell morphology and coloration of subtidal coralline-feeding species (Lindberg, 1983). However, the more conservative (plesiomorphic) characters of *T. virginea* and *T. rosacea,* those of shell structure, gill morphology, and radular basal plate morphology, clearly indicate that these species are members of the clade that we have previously called "*Notoacmea.*"

Although it may be difficult for some workers to imagine *Tectura virginea* and the large, dark *Tectura scutum* as members of the same genus, similar contrasts exist in most other "acmaeid" taxa. For example, consider *Lottia triangularis* (Carpenter, 1864) and *L. pelta. Lottia triangularis* is a small white-shelled, subtidal species with lateral teeth of equal size and shape. *Lottia pelta,* in contrast, is a large, dark-shelled intertidal species with lateral teeth unequal in size and shape. However, both have complex basal plate morphologies, identical shell structure, one pair of marginal teeth, similar gill morphologies, *etc.,* and there is no doubt that *L. triangularis* and *L. pelta* are members of the same clade. The differences between them exist because of adaptations to differences in their habitat not their phylogeny. This is the same situation that occurs in the genus *Tectura*; however, here the type species is the derived subtidal species, not one of the larger, more typical intertidal species.

It is unclear whether the genus *Tectura* as used here is worldwide in distribution or restricted to the Northern Hemisphere. Species groups, with similar radulae and shell structures, have been previously recognized in the Southern Hemisphere (*e.g., Subacmea* and *Conacmea*). However, given the tremendous amount of convergence that occurs in the Lottiidae, it is doubtful that these groupings represent clades. It is unlikely that further study of shells or radulae will yield characters that elucidate phylogenetic relationships in and between regional groups of *Tectura* s.l.; further division of the genus will need to be based on anatomical and biochemical characters.

DISCUSSION

Name changes in the Patellacea have been suggested with increasing frequency over the past 15 yr. After almost 100 yr of usage as a principal genus in the superfamily, *Acmaea* has now become restricted to a single species. Genera that replaced *Acmaea* have themselves been replaced or redefined. Superficially, it appears that "splitting" in the Patellacea has reached epidemic proportions. Why has this occurred?

The main reason for the drastic reallocation and arrangement of the Patellacea is directly due to underestimation of convergence in the taxon. The first worker to provide an insight into the convergence in the superfamily was MacClintock (1967). MacClintock described seven shell structural types in the "Acmaeidae." When he compared gill and radular morphologies with shell structure data, some significant trends became apparent. MacClintock attempted to interpret these trends, but was hampered by a confusing and inaccurate systematic literature.

When limpets are grouped by shell structure, the convergence in radular, gill, and shell characters becomes readily apparent, and usually, these convergences are directly correlated to habitat and (or) history of the taxon. The reason these relationships (and the numerous distinct taxa) were not previously recognized has been due to: (1) the extremely simple morphology of the shell, and (2) the mistaken belief that gill characters were conservative.

The simple shell morphology of the Patellacea has been a problem since the time of Lamarck and Linné. In the late 1700's all mollusks with a limpetlike shell were assigned to the genus *Patella.* As studies were conducted, many taxa were removed from the genus (*e.g., Siphonaria* Sowerby, 1823; *Fissurella* Bruguiere, 1789; *Diodora* Gray, 1821; *Hipponix* Defrance, 1819; *Capulus* Montfort, 1810; *etc.*) (see Powell, 1973:84). The "acmaeids" were one of the last groups to be removed. In this early period there was no attempt to diagnose the patellacean groups on their own characters. They were, and in some cases remain, the residual taxa that are left when non-members are identified and removed. Thus, we have been left with a form taxon, composed of numerous lineages.

It is no accident of history that J. E. Gray is associated with all three taxa discussed above; Gray examined the animals, rather than simply their shells. Every study of a patellacean group that has considered more than shell morphology has led to a better understanding and more taxonomic divisions. Analogous situations have occurred in many other molluscan groups. Consider the genus *Trochus, sensu* Linné, 1758. We no longer consider *Trochus* to be the principal genus in the Trochidae with a worldwide distribution. Instead, we recognize numerous genera, including *Tegula* Lesson, 1835, *Calliostoma* Swainson, 1840, and *Margarites* Gray, 1847, in the northeastern Pacific; *Cantharidus* Montfort, 1810, *Monodonta* Lamarck, 1799, and *Gibbula* Risso, 1826, in the northeastern Atlantic; and *Austrocochlea* Fischer, 1885, *Umbonium* Link, 1807, *Phasianotrochus* Fischer, 1885, and *Chlorodiloma* Pilsbry, 1889, in the austral region. Today, *Trochus* is restricted to the Indo-Pacific and its definition no longer includes

the vast majority of the trochid species. Similar changes are now occurring in the Patellacea.

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